

PHORETIC COPULATION IN HYMENOPTERA

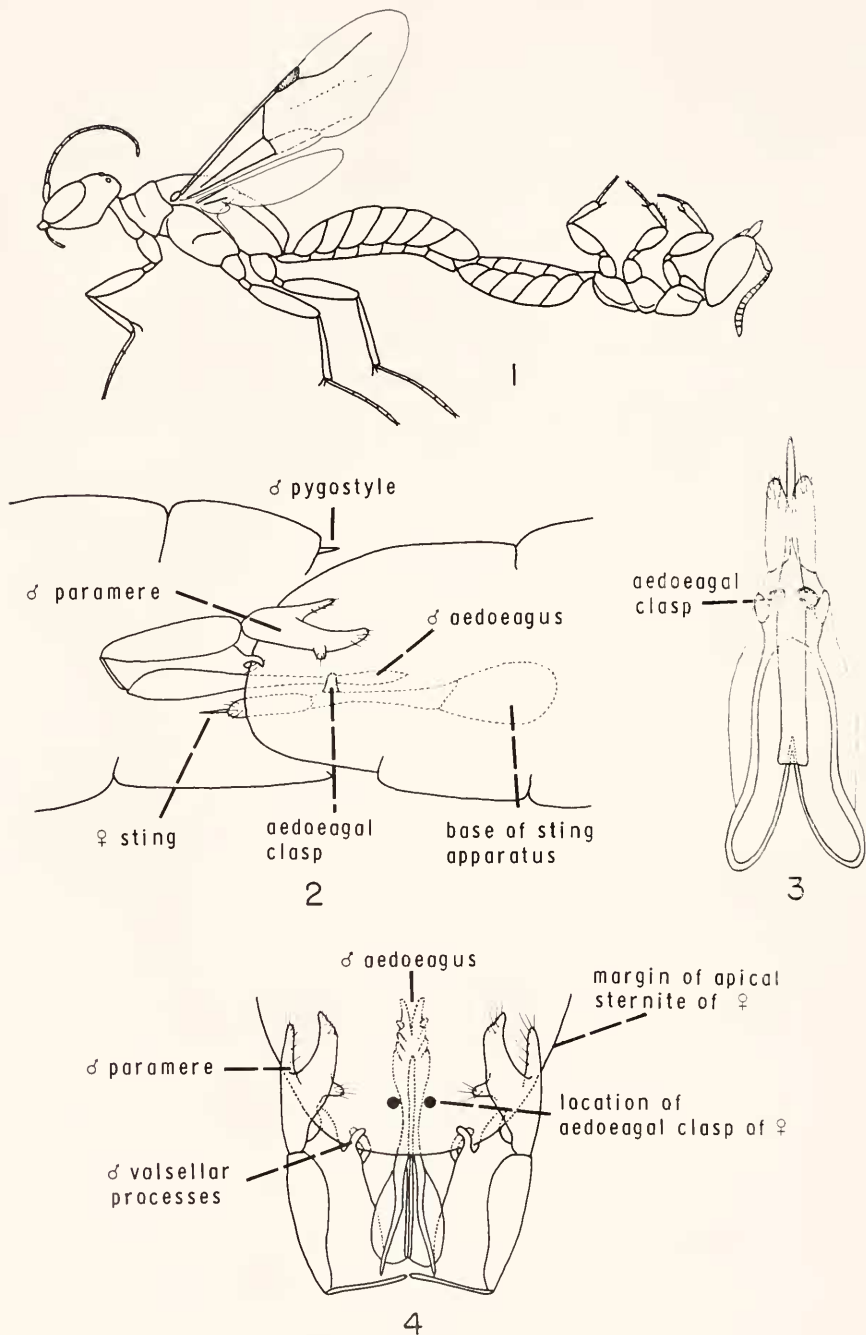
HOWARD E. EVANS¹

ABSTRACT

In several groups of wasps, including members of the families Bethyridae, Tiphidae, and Mutillidae, it is known that the males carry the wingless females about suspended from their genitalia for considerable periods of time. The mechanics of such phoretic copulation have not previously been studied in detail. On the basis of museum specimens pinned *in copulo*, the method of locking of the genitalia is discussed in a bethylid (*Apencsia nitida*) and in two thynnine tiphids (*Dimorphothynnus haemorrhoidalis* and *Elaphroptera scoliiformis*). These three forms show striking differences in the modifications of the male and female genitalia, confirming the belief that phoretic copulation has evolved several times independently. All examples occur in families in which the females are adapted for burrowing in the soil or in wood. Evidently some elements in these families underwent a loss of wings as a further adaptation for hypogaecic life. Several of these stocks independently evolved phoretic copulation, at least partially removing the major disadvantage in flightlessness, namely, decreased capacity for dispersal.

It has long been known that in certain groups of wasps (in all of which the females are wingless and smaller than the males) the sexes remain *in copulo* for a considerable period of time, the males carrying the females about suspended from their genitalia (Figs. 1, 5). It has been assumed that more than copulation is involved, that this prolonged attachment serves in carrying females to feeding sites (at least in the Thynninae) and in aiding in the dispersal of the species (Burrell, 1935; Durán-Moya, 1941). The females in question are highly modified for burrowing through soil or rotting wood in search of their hosts: the legs are relatively short, stout, and spinose; the thorax has various reductions associated with loss of wings; the ocelli are absent and the eyes reduced in size or even vestigial. In some cases the males are known to fly at a considerable height and to carry the females for more than an hour, so it is not unlikely that they do at times scatter the females in such a way that they will find new local populations of their hosts or, given suitable wind currents, cross physical barriers that the females alone would rarely surmount.

¹ Museum of Comparative Zoology, Harvard University, Cambridge, Mass. 02138.



(See caption, bottom p. 115)

Phoretic copulation is best known in the Tiphiidae, especially in the Thynninae (Janvier, 1933; Given, 1954) but also in the Myrmosinae (Krombein, 1956). It has also been reported in the genus *Timulla* of the Mutillidae (Linsley, 1960) and suggested for the genera *Pristocera* and *Dissonaphalus* of the Bethyridae (Evans, 1964). All of these are wasps that attack insects occurring in the soil or in wood and exhibiting a decidedly spotty distribution dependent upon a particular substrate. Thynninae attack scarabaeid larvae, *Pristocera* the larvae of Elateridae (wireworms), Myrmosinae the larvae of ground-nesting bees and wasps, and *Timulla* evidently both wasp and scarabaeid larvae. These groups of wasps are not closely related, and one wonders whether they have evolved similar mechanisms of fastening the genitalia. In fact, how is it possible to achieve so firm an interlocking that the male is able to carry the female for long periods with no other grasp? How is disengagement brought about? Is phoretic copulation a unique phenomenon, or can precedents be found among wasps that are fully winged in both sexes? What can the study of copulating pairs teach us about the function of various parts of the genitalia?

Before attempting to answer these questions, it will be necessary to examine representative pairs in detail, for in fact no one has studied the phoretic mechanism on more than a superficial level. The material available to me consists of museum specimens, dried and mounted on pins, and the muscles and other soft parts are not preserved. These pairs remained together after being killed, with no evident change in the manner of attachment. By relaxing and softening them it is possible to learn a great deal about the interlocking mechanisms, but study of the behavioral aspects of copulation as well as of specimens preserved in a good muscle fixative will be needed to provide complete answers. The available material belongs to the Bethyridae and to two tribes of Thynninae.

Phoretic copulation in the bethylid wasp *Apencsia nitida* (Kieffer). FIG. 1.—A pair as preserved, the male (left) having been mounted on a minuten nadeln. FIG. 2.—Attachment of the male and female enlarged and after drawing the two apart slightly. The male (left) is dorsum-up, the pygostyles being appendages of the apical tergite. The female (right) is venter-up; structures enclosed by the apical sternite of the female are shown as dashed lines. The apical, lateral margins of the last tergite and sternite of the male are omitted for the sake of clarity. FIG. 3.—Sting apparatus of female after dissection from the body (dorsal aspect, sting and sting sheaths uppermost). FIG. 4.—Male genitalia as seen in dorsal view still attached to the apical sternite of the female, the parts located beneath the sternite being shown by dashed lines.

Bethylidae

The cases of prolonged copulation in flight I reported in 1964 were based on indirect evidence in a few species of *Pristocera* and *Dissomphalus*. More recently I have obtained better evidence from a different genus of the same subfamily, *Pristocerinae*. Throughout this subfamily the females are wholly apterous, depressed, short-legged, and often blind or nearly so, in general admirably adapted for entering wood or soil in search of their hosts (often, perhaps always, the larvae of Coleoptera). The new material consists of two pairs of *Apencsia nitida* (Kieffer) taken on a recent expedition of the American Museum of Natural History to South America. Both pairs are labeled Bolivia: Dept. Beni, Rio Itenez, Pampa de Meio, IX-11-13-1964; J. K. Bouseman, J. Lussenhop Collectors. I do not know how the specimens were collected, but the fact that one of them was covered with lepidopterous scales suggests that they may have been taken in a light trap.

The male of this species is 4-5 mm long and is dark brown in color; I redescribed the male from the type in my revision of *Apencsia* (Evans, 1963), and later provided additional locality data and a figure of genitalia (Evans, 1966a). The female is only 2.5 mm long and is light yellowish brown; it is apparently blind, although a smooth interspace between the large punctures near the base of the mandibles may represent a vestigial ommatidium. This is not only the first instance of an American *Apencsia* taken *in copulo*, but the first female *Apencsia* from South America known to science (although 42 species are known from males). Doubtless the females are hypogaedic, perhaps emerging briefly at night to mate and to seek new hosts.

Each pair of *Apencsia nitida* is mounted with a minuten nadeln through the thorax of the male, the female being suspended from the posterior end of the male in an inverted position (Fig. 1). The attachment of the two is broad, and the parameres and other parts of the male genitalia are not visible externally. One assumes that this position is assumed by the male mounting the female dorsally, both individuals facing in the same direction (the most common copulatory posture in wasps), and that upon the male's taking flight the female simply flips backward into a venter-up position.

I placed one pair in a relaxer for 24 hours and then transferred it to 10% KOH for two hours. I then placed it in 50% alcohol and gently lifted the apical tergite of the male to reveal the small pygostyles and the large, trifid parameres, the latter embracing the apical sternite of the female like a three-fingered hand on each side (Figs. 2, 4). I then tried to pull the male and female apart, but without success, as the union was very firm indeed. Further dissection revealed that the apices of the volsellae grasped the edge of the apical sternite of the female like a pair of small pincers, while the aedocagus extended deep inside the female just above

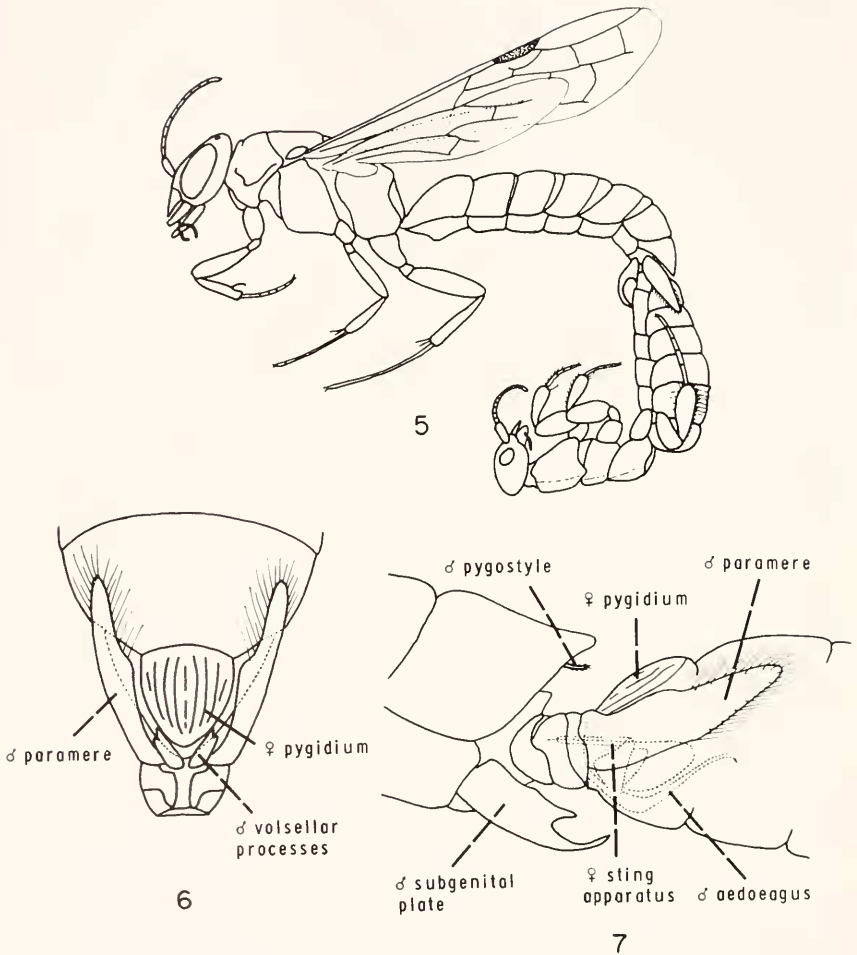
and closely parallel to the sting. Here it was held tightly in place by a pair of sclerotized, pigmented structures suggesting the retinaculum of Collembola, which I shall call the aedoeagal clasps. Only after considerable dissection and manipulation was I able to separate the aedoeagus from the clasps. These clasps evidently arise from the sting sheaths just basad of the apical section and are directed mesad (Fig. 3); they arise from weakly sclerotized bases and the nature of their articulation and musculature (if any) cannot be determined in this material.

I was surprised to find that the aedoeagus assumed quite a different form than previously described. I had previously figured it as considerably shorter and more compact and complex (Evans, 1966a, fig. 3). It is evidently capable of being driven forward by movements of the transverse rods at the base of the genital capsule and their associated muscles; when this occurs various parts apparently slide against one another and some of them project well beyond the apices of the parameres. Furthermore, the extended aedoeagus is constricted at the point of attachment to the aedoeagal clasps and expanded beyond; presumably the somewhat serrated margins of this apical expansion play a role in pushing through the clasps or in holding it fast. So far as I know, such aedoeagal clasps have not previously been described, nor has it been appreciated that the aedoeagus is capable of such great extension and change of form. One would like to know, of course, whether it resumes its usual form following copulation; if not, it is possible that some of the supposed species differences in the aedoeagus may merely represent postcopulatory changes in shape. It is interesting to note that in most genera of Bethyilidae the aedoeagus is of very simple form (see Figures in Evans, 1964); highly complex aedoeagi occur principally in *Pristocera*, *Dissomphalus*, and *Apenesia*; precisely the genera in which phoretic copulation has been reported.

Thynninae

Phoretic copulation apparently occurs in all members of the large tiphiid subfamily Thynninae (I exclude the genus *Dianmma*, which is sometimes placed in a separate subfamily). The females are invariably considerably smaller than the males and not only have the usual reductions in the eyes and in thoracic structures but sometimes have reductions in the mouthparts; the males, in turn, often have modifications of their mouthparts and head capsule which enable them to feed the females (Given, 1954). Given's discussion and sketches indicate that, in the Australian species he studied, the female is attached to the male in a position the reverse of that in *Apenesia*: that is, the female extends behind the male in a dorsum-up position or the bodies of the male and female form a loop so that the female is beneath the male in a venter-up position. Study of museum specimens pinned *in copulo* suggests that this is indeed the usual

condition in Australian species but not in all South American species (as discussed further in a later paragraph).



Phoretic copulation in the thymine wasp *Dimorphothynnus haemorrhoidalis* (Guerin). FIG. 5.—A pair preserved dry, male (left) mounted on a pin. FIG. 6.—Dorsal aspect of end of female abdomen (above) to which male genitalia (below) are still attached. FIG. 7.—Attachment of male (left) and female (right) in lateral view after drawing the two apart slightly. Both are dorsum-up; structures located within the apical segment of the female are shown by dashed lines. Margins of female tergites and sternites are omitted for the sake of clarity.

For purposes of this study I selected a pair of *Dimorphothynnus haemorrhoidalis* (Guérin), a member of the tribe Rhagigasterini. The pair was collected in Geraldton, Western Australia, by P. J. Darlington,

Jr., in October 1931. In this pair the female is suspended downward and forward in the venter-to-venter position common to most Thynninae (Fig. 5). The apical sternite (subgenital plate) of the male has a concave upper surface and a large, hook-shaped terminal spine, fitting closely against the apical sternite of the female. The very large parameres embrace the last two tergites, the grasp enhanced by brushes of stiff setae. In dorsal view, it can be seen that the inner margin of the parameres fits the margin of the pygidial plate closely (Fig. 7). The pair was relaxed and treated in KOH, and with teasing I was able to draw the male and female apart as shown in Figure 7, the extension resulting from a tearing of the membrane at the base of the male genitalia, for the latter remained firmly attached to the female. In this species the apical processes of the volsellae are not hook-like but in the form of elongate folds which are rough on their inner faces; apparently these folds embrace the margin of the apical segment of the female (Fig. 6). The aedoeagus is a simple shaft which is curved up sharply and somewhat attenuate on the apical half; it is non-extensible and only slightly flexible. Its basal part appears to be held against the sternite by the sting apparatus, the lateral plates holding it on each side and a small, transverse phragma (not figured) holding it from above. The sting itself forms a loop, against which the outer part of the aedoeagus fits closely. As in all the forms studied, the sting is somewhat withdrawn and does not extend much beyond the apical segment of the female.

In contrast to *Apensia*, the genitalia of *Dimorphothynnus* have obviously been rotated 280 degrees, so that the ventral surface is uppermost; this is clearly shown by the position of the volsellae. I would assume that the male mounts the female from above in the usual manner, inserting the genitalia and causing them to lock into place; however, instead of merely flipping back into a venter-up position, the female twists 180 degrees so that her dorsum is projected from the dorsum of the male (Fig. 5). When this occurs the male genitalia rotate on their basal membrane. Such a rotation has been described for some of the Chilean Thynninae by Durán-Moya (1941), who however compares them with the Strophandria in the sawflies, a group in which rotation of the genitalia occurs prior to eclosion. In *Dimorphothynnus* and in many other genera of Thynninae, copulating pairs are found to have the male genitalia inverted and to be attached to the male's body primarily by a twisted membrane, while non-copulating males have the genitalia uninverted. In *Dimorphothynnus* the locking device appears to consist of the rigid, angulated aedoeagus, held not by aedoeagal clasps similar to those of *Apensia* but by parts of the sting apparatus itself; the tensile strength of the aedoeagus, combined with the application of the volsellar folds and the three-sided grasp provided by

the large parameres and the subgenital plate, forms a very firm attachment indeed. Because of the inversion of the male genitalia and the body of the female, the aedoeagus is below the sting rather than above it as in *Apneisia*, although the two structures retain the same morphological relationship.

Perusal of museum material reveals that many (if not all) Australian Thyminae copulate with the females in a dorsum-up position, as do many South American forms (the subfamily is confined to those two continents). However, certain South American species copulate with the female in a venter-up position. Janvier (1933, p. 238) has provided an excellent photograph of *Elaphroptera nigripennis* Smith (tribe Thymini) resting on a bush. A pair of this species in the collection of the Museum of Comparative Zoology, pinned through the body of the male, remains in exactly the pose figured by Janvier. Several pairs of *E. scoliiformis* (Haliday) are also preserved in the same pose, the female being suspended venter-up but her body somewhat coiled, in the shape of a U. I relaxed one pair of this species, from Dalcahue, Chiloe, Chile, collected by Luis Peña in January, 1962, and present here a sketch (Fig. 8) and a few comments on the manner of attachment.

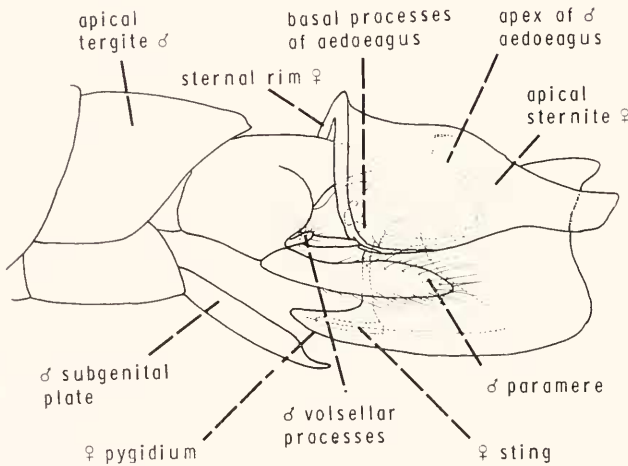


FIG. 8. Attachment of male (left) and female (right) *Elaphroptera scoliiformis* (Haliday) (Thyminae), slightly drawn apart. Drawn from museum specimens, somewhat simplified.

The male of this species possesses heavily sclerotized parameres fringed with setae, as in the preceding example. They embrace the sides of the pygidium much as in *Dimorphothynnus*, although in this case the pygidium is ventral. The subgenital plate of the male is not unlike that

of *Dimorphothynnus*, although with a much smaller apical spine; rather than pressing against the sternum it fits over the pygidial plate. The apical sternite of the female is hood-shaped, and its posterior opening has a broad, sclerotized rim through which the aedoeagus is thrust. The volsellae, however, remain outside this rim, the longer pair of appendages appearing to fit into slots toward the lower part.

The aedoeagus itself is so complex as to defy description. The greater part of it is in the form of a long, somewhat coiled flagellum (which Janvier has figured and aptly compared to the tongue of a lepidopteran). At its base, the aedoeagus is expanded and has various processes, one pair of which is large, flap-like, and directed back toward the base of the genitalia. These evidently push against the sclerotized rim of the sternite from the inside, while a second pair of hook-like processes appears to make a connection with the base of the sting apparatus. The sting itself is small and located close against the pygidial plate, far from the aedoeagus.

Evidently the locking effect is produced by pressure of the volsellae against the sternal rim from the outside opposed to that from the inside provided by the reversed flaps of the aedoeagus; the second pair of hook-like aedoeagal processes may provide added attachment to the sting apparatus. The whip-like part of the aedoeagus plays no obvious role in the locking mechanism; it may penetrate deeply into the spermatheca, but the latter was not preserved in this dried material. Obviously this mechanism would repay much further study. Judging from Janvier's and Durán-Moya's figures, several species of *Elaphroptera* have genitalia of this basic type, but differing in details. In the pair of *E. nigripennis* before me, the apical volsellar lobes are very large, hook-shaped, and curve up so as to embrace the outside of the expanded margin of the apical sternite of the female.

DISCUSSION

In the examples considered here, and probably in most Hymenoptera, the basic function of the major elements in the male genitalia remains the same: the parameres embrace the outside of the apical segment of the female, the volsellar processes (*digitus* and *cuspis*) are associated with holding the margin of the apical segment, and the aedoeagus is thrust deeply into the female, its tip presumably in or near the spermathecal opening. The sting of the female is retracted, though at other times capable of great extension, probably by "taking up the slack" produced by the basal loop.

Wasps exhibiting phoretic copulation have evolved modifications of both sexes so as to provide a remarkably firm interlocking. In the forms studied, the female showed the following specializations: (1) paired,

sclerotized aedoeagal clasps arising from the base of the sting sheaths (*Apencsia*), (2) median and lateral flanges of the sting apparatus, serving to hold the aedoeagus against the arching sternite (*Dimorphothynnus*), (3) a broad, sclerotized rim closing off a large part of the genital opening (*Elaphroptera*, and developed to varying degrees in most Thynninae). In the males, the volsellar processes assume various forms, serving either as clasps (*Apencsia*), as embracing folds (*Dimorphothynnus*), or as struts (*Elaphroptera*). The aedoeagus may be (1) extensible and with a constriction along its shaft (*Apencsia*), (2) rigidly angulate (*Dimorphothynnus*), or (3) whip-like but with complex basal processes, one pair of which is directed basad (*Elaphroptera*).

Whether or not other Bethyridae will be found to possess modifications similar to those of *Apencsia* remains to be seen. In the Thynninae, a scanning of museum material as well as the figures of Durán-Moya (1941), Salter (1958), and others, suggests that in this group the interlocking mechanisms assume many different forms. In fact, the many curious modifications of the male and female terminalia in this group are without parallel in any other group of wasps known to me. It is also remarkable that in most (but not all) genera, the male genitalia twist 180 degrees, apparently after locking with the female has been achieved. This rotation permits the female to feed readily if transported to a source of food by the male (since she is venter-down) or to be fed by the male in any of several ways, since she is able to bend up toward the venter of the male. The structural and behavioral adaptations for feeding described by Given (1954) could not have evolved had not the male genitalia developed the capacity to rotate. Presumably *Elaphroptera* represents a stock of Thynninae in which failed to develop the capacity to rotate the genitalia.

Two important questions cannot be answered: (1) how is separation effected? and (2) do the male genitalia return to their original orientation following copulation? There is no evidence that the male genitalia break away from his body as they do in the honeybee, so it must be assumed that unlocking is possible. Museum specimens not taken *in copulo* always appear to have normal, uninverted male genitalia, so it is probable that these structures do resume their normal orientation (or do the males die after copulating?) Burrell (1935) reported that certain female Thynninae simply "drop to the ground," sometimes while the male is flying more than ten feet high, but no one has described how separation occurs. In the case of *Apencsia*, separation would seem to be fairly simple if, in fact, the aedoeagal clasps are muscled, but how the complex aedoeagus of *Elaphroptera* is withdrawn through the sternal rims of the female is much more difficult to visualize.

It is interesting to speculate as to the possible origin of phoretic copulation. Evidently it has evolved several times independently, and one assumes it has done so because of the selective advantage of dispersing inseminated females into areas where new and unparasitized populations of hosts may be discovered. In each case it has evolved in subfamilies in which winglessness is universal in the female sex. Winged females of Tiphidae and Bethyidae also possess the depressed body form, short, spiny legs, and other adaptations for seeking out hosts in the soil or in wood. Since burrowing adaptations are widespread in these groups and in related families such as the Scoliidae, one assumes they evolved first, and that loss of wings and associated thoracic reductions of the females of certain stocks followed (Reid, 1941). Not only may wings hamper a female burrowing through the soil, but if lost the body materials which go to make up the flight musculature may be redeployed, for example toward the musculature of digging. In a few diverse stocks, there has been evolution toward a smaller relative size of the female and toward the development of diverse modifications of the genitalia permitting the males to carry the females about. In these stocks the major disadvantage of flightlessness, namely, decreased power of dispersal, has been partially cancelled. In some elements in at least one of these stocks, there has developed a rotation of the genitalia such that the females are able to feed or to be fed by the male during the copulatory flight. One assumes that more prolonged phoretic copulation is thus possible.

The reduction in the relative size of the female has an interesting corollary. There is evidence that in many Hymenoptera, fertilized, female-producing eggs are laid on larger prey or in nest-cells containing (on the average) more prey than cells in which unfertilized, male-producing eggs are laid. The result is that in virtually all higher Hymenoptera the females are larger than the males. In the groups exhibiting phoretic copulation, have the females undergone a behavioral reversal such that they lay unfertilized, male-producing eggs on larger prey, fertilized eggs on smaller prey? Or do female larvae fail to consume all their food?

Finally, we should ask if there are instances of fully winged Hymenoptera exhibiting phoretic copulation. Hymenoptera, indeed insects in general, show much variation in the amount of time required for mating, and I am not aware that it is known why some species are able to effect insemination in a few seconds, others only after many minutes. Several species of wasps which are fully winged in both sexes are known to remain *in copulo* for many minutes and, if disturbed, to fly about, the larger female usually pulling the male behind her attached by the genitalia. Such behavior has been described in the eumenid wasp *Monobia quadridens* by Rau (1935) and in the sphecid wasp *Sphex speciosus* by Lin

(1966). Lin has provided photographs of mating pairs and has conjectured that prolonged copulation may have evolved "as an adaptation to conspecific interference by rival males" in this gregarious species. He suggests that the capacity to fly during mating may represent an escape mechanism from predators during this period of high vulnerability. The method of attachment of males and females in *Sphécus* has not been studied, but the shape of the male volsellar processes is suggestive of a hooking mechanism (Evans, 1966b, p. 11).

Of course, eumenids and sphecids are by no means ancestral to the tiphiids and bethylids discussed earlier, and we presently know of no cases of what might be called "facultative phoretic copulation" among these more primitive wasps. However, the situation in *Sphécus* and *Monobia* suggests that the potential exists and permits us to postulate other factors—rivalry of males and escape from predators—which may have been operative during the perfection of these elaborate locking mechanisms.

REFERENCES CITED

- BURRELL, R. W. 1935. Notes on the habits of certain Australian Thynnidae. Jour. New York Ent. Soc., 43: 19-28.
- DURÁN-MOYA, L. 1941. Die Thynniden Chiles. Arch. Naturgesch., (n.f.) 10: 71-176.
- EVANS, H. E. 1963. A revision of the genus *Apencsia* in the Americas (Hymenoptera, Bethyridae). Bull. Mus. Comp. Zool., 130: 251-359.
- . 1964. A synopsis of the American Bethyridae (Hymenoptera, Aculeata). Bull. Mus. Comp. Zool., 132: 1-222.
- . 1966a. Further studies on neotropical Pristocerinae (Hymenoptera, Bethyridae). Acta Hymen., 2: 99-117.
- . 1966b. The Comparative Ethology and Evolution of the Sand Wasps. Harvard University Press, 526 pp.
- GIVEN, B. B. 1954. Evolutionary trends in the Thynninae (Hymenoptera; Tiphiidae) with special reference to feeding habits of Australian species. Trans. R. Ent. Soc. London, 105: 1-10.
- JANVIER, H. 1933. Étude biologique de quelques Hyménoptères du Chili. Ann. Sci. Nat., Zool., (10)16: 209-355.
- KROMBEIN, K. V. 1956. Biological and taxonomic notes on the wasps of Lost River State Park, West Virginia, with additions to the faunal list. Proc. Ent. Soc. Washington, 58: 153-161.
- LIN, N. 1966. Courtship behavior of the cicada killer wasp, *Sphécus speciosus*. Animal Behaviour, 14: 130-131.
- LINSLEY, E. G. 1960. A fragmentary observation on the mating behavior of *Timulla*. Pan-Pacific Ent., 36: 36.
- RAU, P. 1935. The courtship and mating of the wasp, *Monobia quadridens* (Hymen.: Vespidae). Ent. News, 46: 57-58.
- REID, J. A. 1941. The thorax of the wingless and short-winged Hymenoptera. Trans. R. Ent. Soc. London, 91: 367-446.
- SALTER, K. E. W. 1958. Studies on Australian Thynnidae Shuckard, 1841 (Hymenoptera). III. An introduction to the comparative morphology of the male. Proc. Linn. Soc. New South Wales, 82: 328-351.